

Leg-chaetotaxy with special reference to the *Pterygosomidae* (Acarina)

by

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This essay has grown out of some detailed observations on the chaetotaxy of the legs in the genus *Geckobia*, undertaken originally with a view to providing diagnostic characters to the many species of that genus. Extension of the observations to the other genera of the *Pterygosomidae* has afforded me so much of interest and delight that the temptation to discuss the preliminary observations has proved irresistible. The study has also provided much food for thought and speculation, some of which is included as foci for discussion rather than as confident hypotheses. Relatively few observations have been made, especially of males and immature stages and no detailed analysis of infra-specific variation has been attempted. The work of Goksu, Wharton and Yunker (1960) on such variation in laboratory-reared populations of *Trombicula* (*Leptotrombidium*) *akamushi* amply demonstrates the folly of too-easy acceptance of setation patterns. Certainly such variation does occur often as loss or duplication of one or more setae. However, it commonly affects only one leg and is easily recognized in the majority of cases.

While much of the material discussed here is directly relevant to taxonomy, this is not the primary object of the essay. Important taxonomic data have been intentionally omitted as such is readily obtainable from the works listed in the bibliography. Especial mention must be made however of the fine studies by Dr R. F. Lawrence himself on the *Pterygosomidae* of South Africa which, together with the work of Mr A. S. Hirst and Mr F. Cunliffe, have supplied invaluable information on the habit of these parasites. References to important work on chaetotaxy have been omitted in the main as a useful list has been given already by Dr R. V. Southcott (1961).

The *Pterygosomidae* are a natural family of prostigmatic scale-mites, comprising some 120 species, unequally distributed between seven genera (eight if *Pimeliaphilus* Trägårdh (1905) is included. This anomalous genus was reviewed recently (Jack, 1961) and its removal from the *Pterygosomidae* to the *Raphignathidae* s.lat. was proposed.

Most of the species are to be found in the genera *Geckobia* Megnin (1878), *Pterygosoma* Peters (1849), and *Zonurobia* Lawrence (1935). The remaining genera, namely *Scaphothrix* Lawrence (1935), *Ixodiderma* Lawrence (1935), *Geckobiella* Hirst (1917) and *Hirstiella* Berlese (1920) have fewer representatives.

The scale-mites are characterized by the absence of both genital suckers and of pulvilli from the legs; in having freely projecting peritremes at the base of the gnathosoma; having a pedipalp with the ventral tarsus forming a thumb-claw process with the palp-tibia and in having a distorted movable digit to the chelicera, which acts both as a penetrating organ and as a means of anchorage on the host. The family shows affinities, via *Pimeliaphilus* Trägårdh (1905), to the *Raphignathid-Stigmaeid* group.

The *Pterygosomidae* live as parasites on lizards whose body fluids they suck. To this end they show varying degrees of structural modification to the chelicerae, the body form, the relative positioning of the legs and of idiosomal hypertrichy. The least specialized genus appears to be *Hirstiella* and its least specialized member *Hirstiella insignis* Berlese (1892). To complete the background picture, the salient features of the different genera are reviewed in the paragraphs immediately following.

Hirstiella Berlese (1920) occurs in Mexico, California, Colombia, Italy, Morocco and India on quite different genera of iguanid and geckonid lizards, though each species appears to be quite specific to its lizard host. The body is always longer than wide, the anterior two pairs of legs widely separated from the posterior two pairs which project postero-laterally. The idiosomal setae are few, arranged in transverse rows, a feature found only in the larval stages of the other genera. The mouthparts are terminal and relatively large. The pedipalpal thumb-claw process is larger than usual in the family. All of these features appear consonant with a primitive free-living type. Within the genus the different species show progressive shortening of the legs, from *H. insignis* Berlese (1892) where the legs are long and slender (fig. 5) to those of *H. stamii* Jack (1961) where they are relatively short and blunt, resembling those of the more specialized genera. On morphological grounds alone one might suggest that this genus houses forms which are true scale-mites and others, particularly *H. insignis* and to a lesser extent *H. tenuipes* Hirst (1917), which lead an epizootic or sporadically ectoparasitic life on the lizard. The legs and long setae of *H. insignis* seem more fitted for highly mobile forms such as *Damaeus* rather than to a parasite. The occurrence of this species in the 'pli anale' recorded by André (1961) and Cunliffe's record (1952) of *H. trombidiformis* from a cave in Mexico supports the view that these species are scale-mites more by courtesy than by habit. The chelicerae also show correlated variation. In *H. insignis* they are adapted to piercing rather than to piercing and anchorage. Similarly the dorsal body setae appear to become smaller as the parasite becomes more truly a scale-mite. In view of these differences one may well sympathise with the action of Vitzthum (1943) in proposing the genus *Pimeliaphiloides* for *H. insignis*. For the present however I would agree with Cunliffe (1952) in retaining this species in *Hirstiella*.

Geckobiella Hirst (1917) comprises only two species, *G. texana* Banks (1904) and *G. harrisi* Davidson (1958). The former occurs on many species of the iguanid genus *Sceloporus* in Mexico and the southern United States of America, the latter is found on *Plica plica* from Brazil. This genus is adapted to live beneath the relatively

small scales of the host. *Geckobiella texana* retains the normal dorso-ventral orientation on the host, attaching to the deep-lying, soft skin between two adjacent scales so that the elongate body is protected by one or other of them. *Geckobiella harrisi* however shows a more specialized method of fixation in that the body lies on its side, attached to the pedicel of the scale, with the body of the mite lying across the longitudinal axis of the host body, protected by two adjacent scales (Davidson, 1958, fig. 3).

Essentially the same end is attained, but in quite a different way, in the four genera *Scaphothrix* Lawrence (1935), *Zonurobia* Lawrence (1935), *Pterygosoma* Peters (1849) and *Geckobia* Megnin (1878). These genera lead a more or less sedentary existence, as adult females at least, protected beneath a single scale of the host. In all four genera this involves a great increase in body width, a process for which Dr F. A. Turk, elsewhere in this volume, has coined the term *allocotogenesis*. Correlated with this allometric growth, the legs become shorter and more closely grouped together to lie alongside the mouthparts, all projecting antero-laterally. *Scaphothrix* retains the primitive condition of having few setae, totalling 13 pairs on the whole idiosoma. This same number commonly occurs on the larvae of most genera, where they are restricted to the dorsal body surface. In *Scaphothrix* however 5 pairs are inserted ventrally.

The other three genera show more or less marked idiosomal hypertrichy, an increase in the number of dorsal body setae and also of ventral setae in the case of *Geckobia* and to a lesser extent *Zonurobia*. Not surprisingly however in these large genera, some species are encountered which adapt to their parasitic life in ways other than this typical method. For example *Zonurobia sanguinolenta* Lawrence (1935) and *Z. subquadrata* Lawrence (1935) are described as attaching with the ventral surface uppermost. The idiosoma of these species is more circular in outline than in many other species and it seems likely that they may attach with the body more or less exposed, tick-like.

The same condition is found in a number of *Pterygosoma* species, e.g. *P. caucasica* Jack (1960), *P. gracilipalpis* Jack (1962) and *P. dracoensis* Jack (1962). These species too attach with the body more or less exposed or else in situations where scales are lacking. Thus *P. gracilipalpis* is recorded from the cloaca of *Agama tuberculata* and *P. dracoensis* from beneath the 'wings' of flying lizards of the genus *Draco*.

In *Ixodiderma* Lawrence (1935) this method is typical of the genus as a whole and represents the third type of parasitic specialisation in the family. This latter genus and the exceptions mentioned above are all mites with a tough, more or less leathery cuticle and well developed chelicerae. They attach in exposed situations between the scales or in regions devoid of scales, anchored solely by the gnathosoma, which in the cases of *Ixodiderma* is further specialized by the development of a curious fleshy pad (Lawrence 1935, figs. 13-15, 17-18). *Ixodiderma inverta* Lawrence (1935), like the *Zonurobia* species mentioned above, attaches with the ventral surface uppermost, an obvious example of convergent adaptation.

The same habit of leaving much of the body exposed is commonly found in

the genus *Geckobia* and is recorded by Hirst (1917, 1926), Trägårdh (1905) and Lawrence (1936). In this genus some species attach to the toes rather than beneath the body scales. Such species, e.g. *G. simplex* Hirst (1926), usually have a globular or circular, disc-like idiosoma and retain a thin cuticle, so differing from the genera mentioned above. Even the species which show allocotogenesis however and which normally attach beneath scales also occur quite often on the dorsal surface of the host, behind the tubercles commonly found on many geckos. It is probably significant in this connection that the average size of mature females in the genus *Geckobia* is much less than that of the other genera of *Pterygosomidae*.

The legs in the *Pterygosomidae* are characteristically five segmented, though in *Hirstiella insignis* Berlese (1892) there is a trace of division into basitarsus and telotarsus. The coxae are immovable, fused to the ventral body surface. On each side of the body, coxae I and II are fused to form the anterior common coxal plate, similarly coxae III and IV together form the posterior common coxa. The setation pattern found on the tibia, genu, femur and trochanter is simpler and more easily represented than that of the tarsus some aspects of which will be considered later.

Fig. 1 shows a diagrammatic representation of the setal distribution on these proximal podomeres in each genus. Each rectangle represents a podomere seen from above, extended at right angles to the longitudinal axis of the body, with the head towards the left of the page. Black discs indicate the position of ventral setae, white circles indicate dorsal setae and half-black discs indicate lateral setae, those on the left being antero-lateral and those on the right postero-lateral. I am indebted to Dr G. O. Evans for this simple but effective means of plotting leg setation patterns. In fig. 1 the maximum number of leg setae occurring in each genus is recorded. It is immediately apparent that the different patterns can be derived by progressive loss of certain setae. That this interpretation is more likely than the converse is indicated by the relatively unspecialized genus *Hirstiella* and by comparison with free-living members of related families, e.g. *Pimeliophilus cunliffei** Jack (1961) (fig. 1).

It is perhaps significant that the characteristically African genera *Zonurobia*, *Ixodiderma* and *Scaphothrix* all show loss of the lateral pair of setae on tibiae II, III and IV, a condition which they share with *Pterygosoma*, a more widespread genus.

In each genus variation occurs on the generic pattern shown in fig. 1. These variations are summarized in table 1 which shows the number of setae on the legs of the scale-mite species investigated. Each bracketed number refers to the number of setae on a podomere, e.g. the tibia, of legs I to IV in succession. The brackets refer to the tibia, genu femur and trochanter in this order. Such variation is seen, for example in *Geckobiella* where *G. harrisi* Davidson (1958) differs from *G. texana*

* The name *Pimeliophilus cunliffei* was proposed in 1961 for *P. podapolipophagus* of Cunliffe (1952) and Baker & Wharton (1952), which is not conspecific with *P. podapolipophagus* Trägårdh (1905). I am obliged to Dr C. Yunker for pointing out that a holotype should be designated. The holotype is on a single slide carrying females, males and a larva. The mount was kindly loaned by Dr. E. W. Baker.

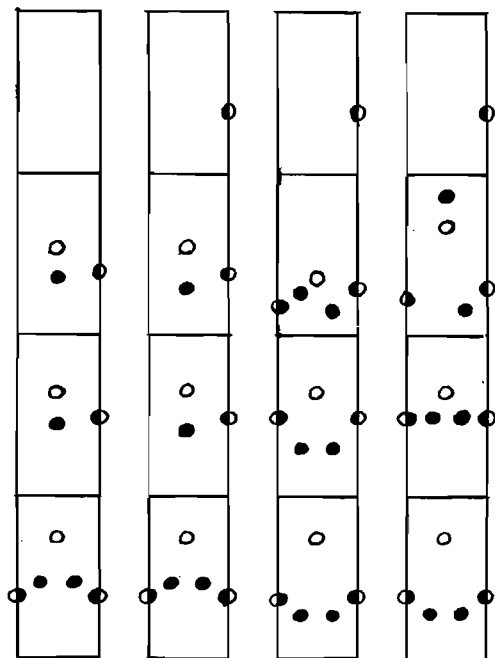
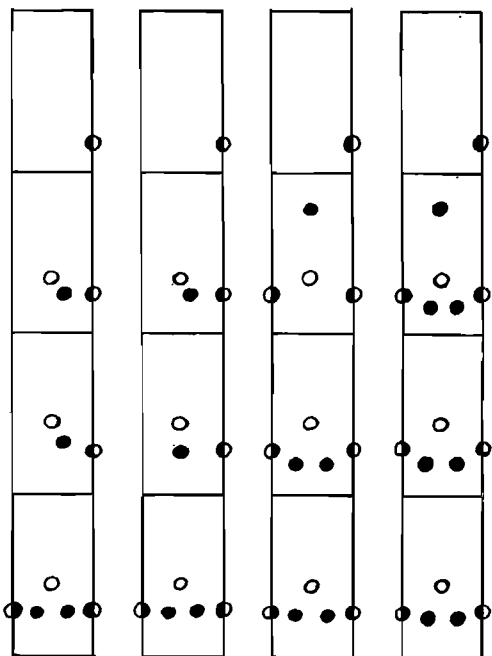
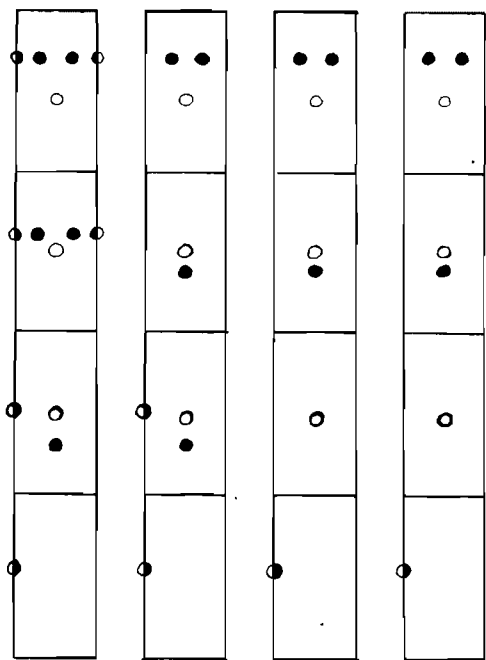
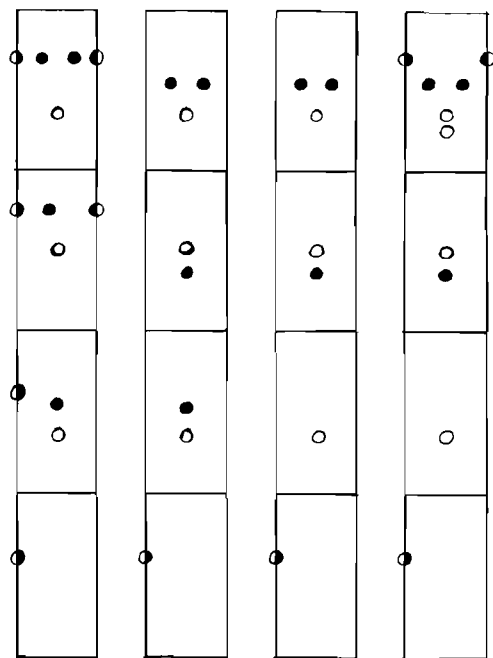
*Pimeliaphilus cunliffei* Jack, 1961*Hirstiella trombidiformis* Berlese, 1920*Ixodiderma pilosa* Lawrence, 1935*Scaphothrix convexa* Lawrence, 1935

Fig. 1.—For explanation see fig. 1, second continuation.

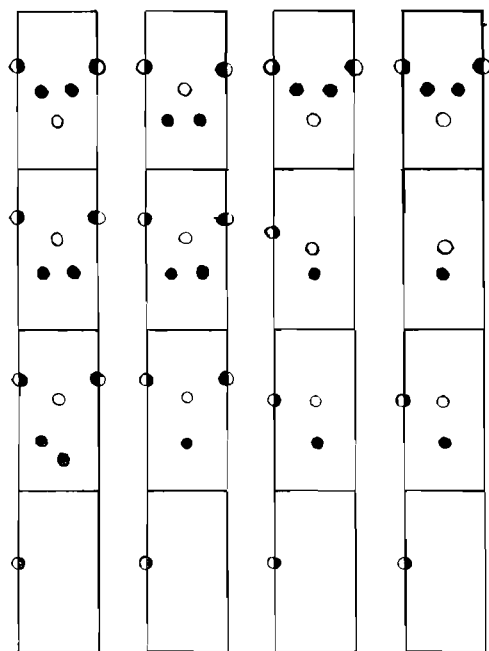
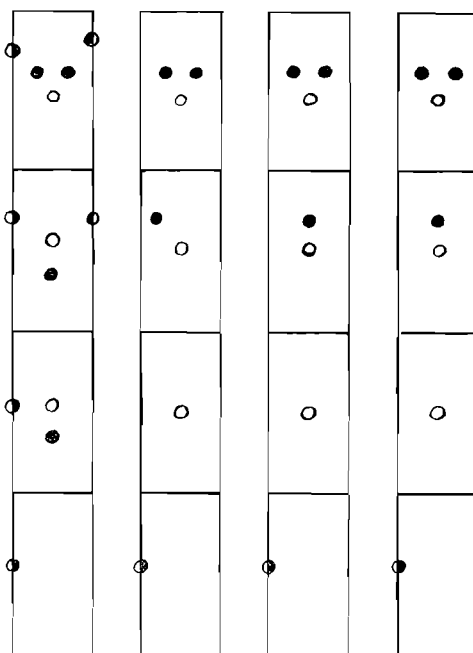
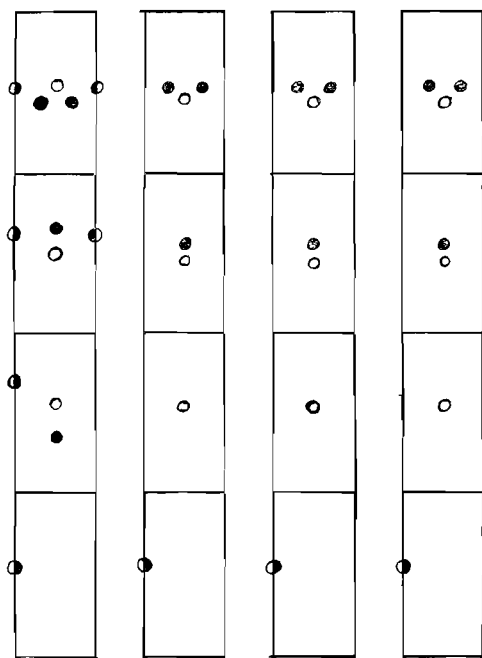
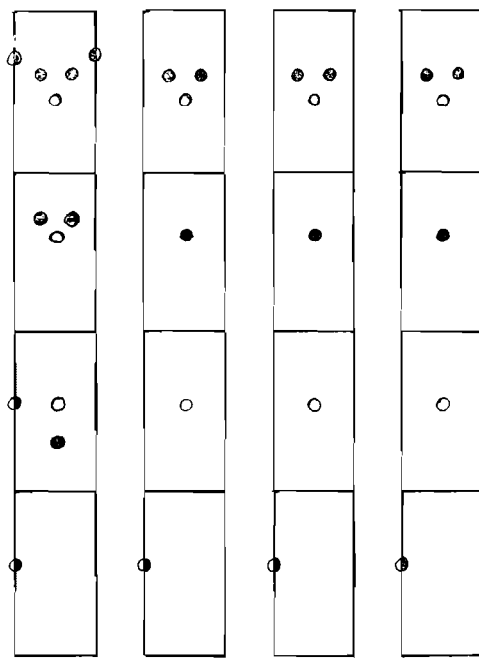
*Geckobiella texana* (Banks, 1904)*Zonurobia transvaalensis* Lawrence, 1935*Pterygosoma (Gerrhosaurobia) hystrix*
Lawrence, 1935*Pterygosoma* group 1 (Table 1)

Fig. 1 continued.—For explanation see fig. 1, second continuation.

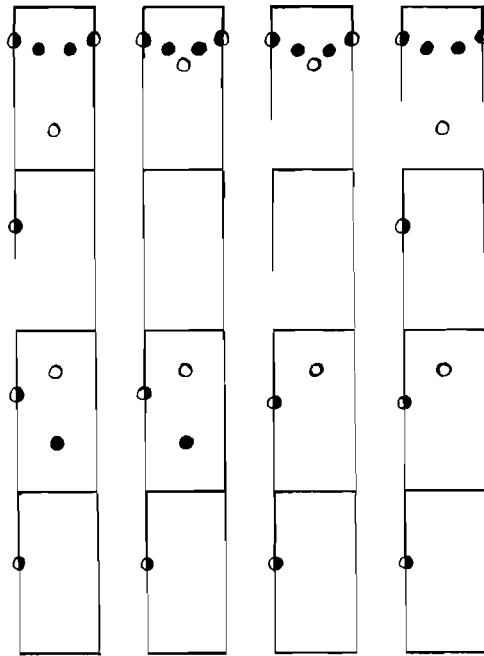
*Geckobia boulengeri* Hirst, 1917

Fig. 1, second continuation.—Diagram to show distribution of setae on tibia, genu, femur and trochanter of the genera of Pterygosomidae. ○ dorsal setae, ● ventral setae, ◐ antero-lateral setae, ◑ postero-lateral setae.

Banks (1904) in the loss of the following setae: the lateral pair of tibiae II-IV; the ventral pair of genu II; the antero-lateral seta of genu III and the ventral of femur IV. The similarity between the setation of the tibiae in *Geckobiella harrisi* and the African genera mentioned above is probably a case of convergence. Firstly *Geckobiella* occurs in the New World only, while *Pterygosoma* and the typical African genera do not. Secondly the setation patterns of femora I and II in *Geckobiella* is quite different from that found in the group *Pterygosoma-Ixodiderma-Scaphothrix-Zonurobia*.

Table 1.—Summary of leg chaetotaxy of the tibiae trochanters in Pterygosomidae.

<i>Hirstiella</i>									
<i>H. trombidiformis</i>	(5-5-5-5)	(5-5-3-3)	(5-5-3-3) (1-1-1-0)=55
<i>H. insignis</i>	(5-5-5-5)	(5-5-3-3)	(5-5-3-2) (1-1-1-1)=55
<i>H. tenuipes</i>	(5-5-5-5)	(5-5-3-3)	(5-4-3-2) (1-1-1-0)=53
<i>H. stamii</i>	(5-5-5-5)	(5-3-2-2)	(2-2-2-1) (1-1-1-1)=43
<i>Geckobiella</i>									
<i>G. texana</i>	(5-5-5-5)	(5-5-3-2)	(5-5-3-3) (1-1-1-1)=55
<i>G. harrisi</i>	(5-3-3-3)	(5-3-2-1)	(5-3-2-1) (1-1-1-1)=40

<i>Ixodiderma</i>									
<i>I. pilosa</i>	(5-3-3-3)	(5-2-2-2) (3-3-1-1) (1-1-1-1)=37
<i>I. lacertae</i>	(5-3-3-3)	(5-3-2-2) (3-2-1-1) (1-1-1-0)=36
<i>I. inverta</i>	(5-3-3-3)	(5-2-2-2) (3-1-1-1) (1-1-1-1)=35
<i>Scaphothrix</i>									
<i>S. convexa</i>	(5-3-3-3)	(4-2-2-2) (3-2-1-1) (1-1-1-1)=35
<i>Zonurobia</i>									
<i>Z. group 1</i>	(5-3-3-3)	(4-2-2-2) (3-1-1-1) (1-1-1-1)=34
<i>Z. cordylensis</i>	(5-3-3-3)	(3-2-2-2) (3-1-1-1) (1-1-1-1)=33
<i>Z. group 2</i>	(5-3-3-3)	(3-1-1-2) (3-1-1-1) (1-1-1-1)=31
<i>Z. group 3</i>	(5-3-3-3)	(2-1-1-2) (3-1-1-1) (1-1-1-1)=30
<i>Pterygosoma Gerrhosauroida</i>									
<i>P. (G.) hystrix</i>	(5-3-3-3)	(4-2-2-2) (3-1-1-1) (1-1-1-1)=34
<i>P. (G.) bicolor</i>	(4-2-3-2)	(4-1-1-2) (3-1-1-1) (1-1-1-1)=29
<i>Pterygosoma Pterygosoma</i>									
<i>P. fimbriata problematica</i>	(5-3-4-3)	(3-1-1-1) (3-1-1-1) (1-1-1-1)=31
<i>P. group 1</i>	(5-3-3-3)	(3-1-1-1) (3-1-1-1) (1-1-1-1)=30
<i>P. neumanni</i>	(5-3-3-3)	(3-1-1-0) (3-1-1-1) (1-1-1-1)=29
<i>P. benguelae</i>	(5-3-3-3)	(3-1-0-1) (2-1-1-1) (1-1-1-1)=28
<i>P. group 2</i>	(5-3-3-3)	(3-0-0-1) (3-1-1-1) (1-1-1-1)=28
<i>P. group 3</i>	(5-3-3-3)	(2-0-0-1) (3-1-1-2) (1-1-1-0)=27
<i>P. group 4</i>	(5-3-3-3)	(3-0-0-0) (3-1-1-1) (1-1-1-1)=27
<i>P. transvaalensis</i>	(5-3-3-3)	(2-0-0-0) (3-1-1-1) (1-1-1-1)=26
<i>P. dracoensis</i>	(5-3-3-3)	(0-0-0-0) (3-1-1-1) (1-1-1-1)=24
<i>Geckobia</i>									
<i>G. boulengeri</i>	(5-5-5-5)	(1-0-0-1) (3-3-2-2) (1-1-1-1)=36
<i>G. group 1</i>	(5-5-5-5)	(1-0-0-1) (3-2-2-2) (1-1-1-1)=35
<i>G. diversipilis</i>	(5-5-5-5)	(0-0-0-1) (3-2-2-2) (1-1-1-1)=34
<i>G. indica</i>	(5-5-5-5)	(1-0-0-0) (3-2-2-2) (1-1-1-1)=34
<i>G. gymnodactyli</i>	(5-5-5-5)	(1-0-0-1) (3-2-1-2) (1-1-1-1)=34
<i>G. simplex</i>	(5-5-5-5)	(1-0-0-1) (2-2-2-2) (1-1-1-1)=34
<i>G. gleadowiana</i>	(5-5-5-5)	(0-0-0-0) (3-2-2-2) (1-1-1-1)=33
<i>G. australis</i>	(5-5-5-5)	(1-0-0-1) (2-1-2-2) (1-1-1-1)=33
<i>G. socotrensis</i>	(5-5-5-5)	(0-0-0-1) (2-1-2-2) (1-1-1-1)=32
<i>G. group 2</i>	(5-5-5-5)	(1-0-0-0) (2-1-1-1) (1-1-1-1)=30
<i>G. oedurae</i>	(5-5-5-5)	(0-0-0-0) (2-1-1-2) (1-1-1-1)=30
<i>G. keegani</i>	(5-5-5-5)	(0-0-0-0) (2-1-1-1) (1-1-1-0)=28
<i>G. group 3</i>	(4-4-4-5)	(0-0-0-0) (2-1-1-2) (1-1-1-1)=27
<i>Zonurobia group 1:</i>	<i>Z. transvaalensis</i> , <i>Z. polyzonensis</i> , <i>Z. debilipes</i> , and <i>Z. semilunaris</i> .								
<i>Zonurobia group 2:</i>	<i>Z. sanguinolenta</i> , <i>Z. subquadrata</i> , <i>Z. circularis circularis</i> , <i>Z. circularis longipilis</i> , <i>Z. circularis capensis</i> , <i>Z. circularis latior</i> .								
<i>Zonurobia group 3:</i>	<i>Z. circularis spiniventer</i> , <i>Z. montana</i> .								
<i>Pterygosoma group 1:</i>	<i>P. persicum</i> , <i>P. bibronii bibronii</i> , <i>P. bibronii pseudorbicularis</i> , <i>P. agamae</i> , <i>P. crewei</i> , <i>P. tuberculata</i> , <i>P. melanum longipalpe</i> , <i>P. melanum angolae</i> .								
<i>Pterygosoma group 2:</i>	<i>P. spinosa</i> , <i>P. serrata</i> , <i>P. tenuisetis</i> , <i>P. caucasica</i> , <i>P. mutabilis</i> , <i>P. inermis inermis</i> , <i>P. adramitana</i> .								
<i>Pterygosoma group 3:</i>	<i>P. annectans</i> , <i>P. annectans circularis</i> .								
<i>Pterygosoma group 4:</i>	<i>P. sinaita</i> , <i>P. foliosetis</i> .								
<i>Geckobia group 1:</i>	<i>G. pachydactyli</i> , <i>G. damarensis</i> , <i>G. fitzsimonsi</i> , <i>G. karrooica karrooica</i> , <i>G. karrooica draconensis</i> , <i>G. hemidactyli</i> , <i>G. hewitti</i> , <i>G. homopholis</i> , <i>G. phyllodactyli</i> , <i>G. tasmani</i> , <i>G. tarentulae</i> , <i>G. loricata</i> , <i>G. latasti</i> , <i>G. hindustanica</i> , <i>G. malayana</i> , <i>G. turkestanica</i> , <i>G. gehyrae</i> , <i>G. papuana</i> , <i>G. philippinensis</i> , <i>G. clelandi</i> .								
<i>Geckobia group 2:</i>	<i>G. haplodactyli</i> , <i>G. naultina</i> .								
<i>Geckobia group 3:</i>	<i>G. rhotropi</i> , <i>G. transvaalensis</i> , <i>G. namaquensis</i> , <i>G. ovambica</i> , <i>G. capensis capensis</i> , <i>G. capensis lanceolata</i> , <i>G. capensis hastata</i> .								

Ixodiderma lacertae differs from *I. pilosa* shown in fig. 1 by the loss of the antero-lateral setae of femur II and trochanter IV and in the presence of an antero-lateral seta on genu II. *Ixodiderma inverta* lacks both the antero-lateral and the ventral setae on femur II. However, because of the peculiar orientation of the legs in this

particular genus, with the plane of the coxae perpendicular to the plane of the mouth-parts, observation of the leg setae is rather difficult. Dissection of an adequate number of specimens is desirable and has been attempted on two specimens of different species. However, the quantity of available material debarred further dissections. In consequence the observations on this genus are more susceptible to error.

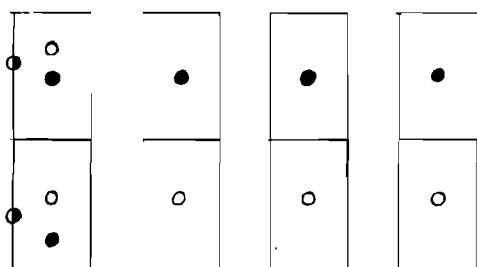
The same is true for *Scaphothrix*. Here again material is limited. Furthermore, for some reason, the legs of all available specimens show damage to the cuticle and loss of leg setae. The observations recorded are based on the location of seta-bases in a number of individuals.

In *Pterygosoma* so far as my observations go, the pattern of tibial and trochanteral setation remains constant except in *P.annectans* Jack (1962) and *P.annectans circularis* Jack (1962), where the antero-lateral seta of trochanter IV is lost. The variation in chaetotaxy of the genu and femur of each leg is shown in fig. 2. The subgenus *Gerrhosauroidia* Lawrence (1958) is quite different. Unfortunately *P.(G.) gerrhosauri* Lawrence (1935), the type species, is not available for examination. *Pterygosoma (G.) hystrix* Lawrence (1935) and *P.(G.) bicolor* Lawrence (1935) show quite marked differences as shown in fig. 1 and table 1. The existence of such differences supports Dr Lawrence's (1958) division of the genus into two subgenera.

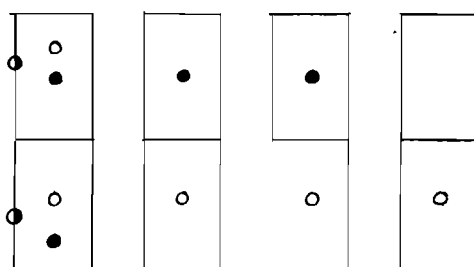
Similarly in *Geckobia* the setation of the tibia and trochanter is more or less constant, resembling that shown in fig. 1 except in *G.keegani* Lawrence (1953) which lacks the antero-lateral seta of trochanter IV and in the group formed by *G.rhoptropi*, *G.transvaalensis*, *G.namaquensis*, *G.ovambica*, *G.capensis capensis*, *G.capensis lanceolata* and *G.capensis hastata* (Lawrence, 1936, 1951), each of which has lost the antero-lateral setae of tibiae I-III inclusive. It seems very likely that this indicates relationship within this group rather than convergence. The setation of the genu and femora of the *Geckobia* species studied with respect to leg setation is shown in fig. 3.

Of all genera of *Pterygosomidae*, however, the most interesting in this connection is *Hirstiella*. Mention has been made above of the wide geographical distribution of this genus and its equally wide host distribution. All this be it noted in a genus which at present totals only eight species, each represented by one or at most a very few records. There are sufficient morphological grounds to assert that there is a greater range of habit in this small genus than in any of the larger genera of more specialized forms. Unfortunately it is not possible to give details of the chaetotaxy in all species. However, those available have been summarized in table 1 and shown in fig. 4; that of *Hirstiella trombidiformes* is shown again to facilitate comparison. Examination of the setal pattern in these four species shows that in this character too there is considerable variation, both in number of setae and in their spatial distribution, in their size and form. It seems very likely that many more species of *Hirstiella* await description.

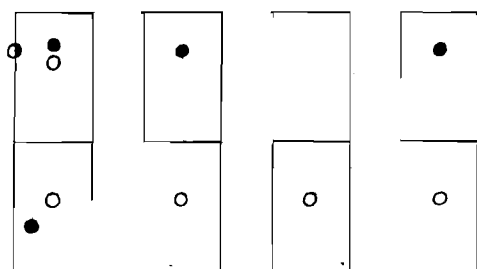
In a way the genus *Hirstiella* shows the same story as the family *Pterygosomidae* writ small. Within the series of species from *H.insignis* to *H.stamii* mentioned above there is a corresponding progressive loss of leg setae. The legs of *H.insignis* are very long (fig. 5), the segments attenuated, contorted and flattened at the joints. In consequence there is little space for insertion of the setae, which are surprisingly



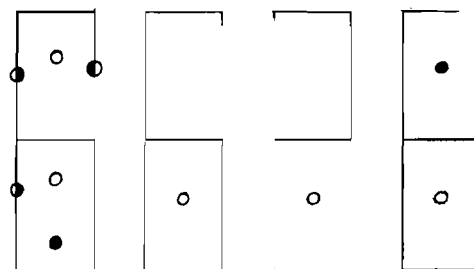
P. fimbriata problematica Jack, 1962 and
P. group 1 (Table 1)



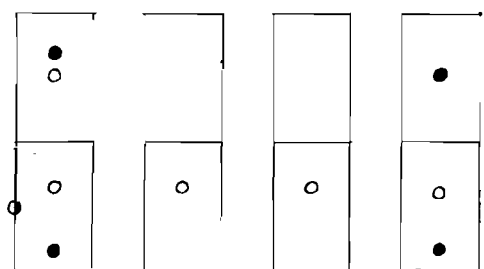
P. neumanni Berlese, 1910



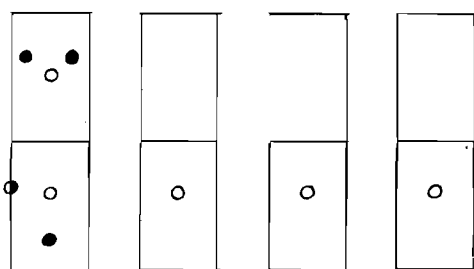
P. benguellae Jack, 1962



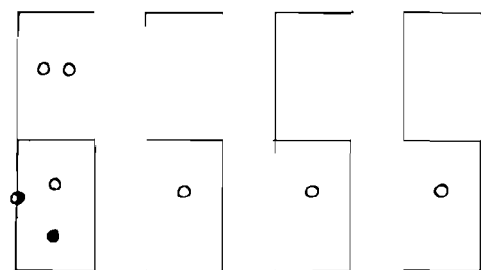
P. group 2 (Table 1)



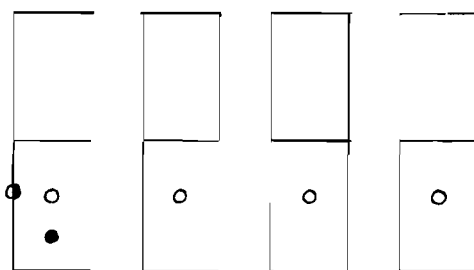
P. group 3 (Table 1)



P. group 4 (Table 1)



P. transvaalensis Lawrence, 1936



P. dracoensis Jack, 1962

Fig. 2.—Variation of chaetotaxy of the genu and femur in the genus *Pterygosoma* Peters, 1849.

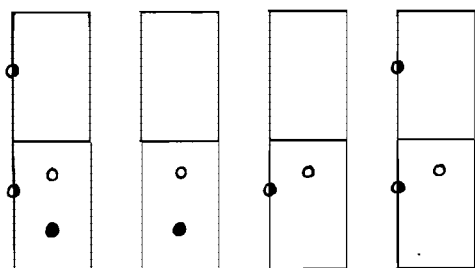
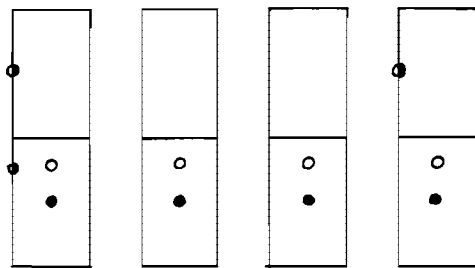
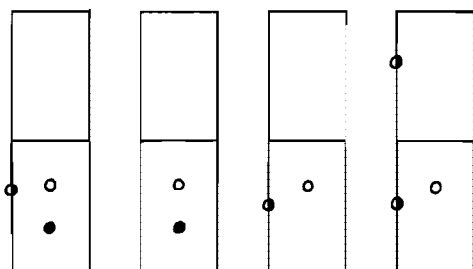
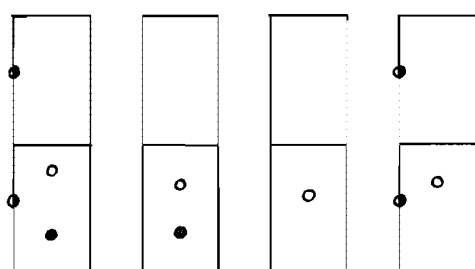
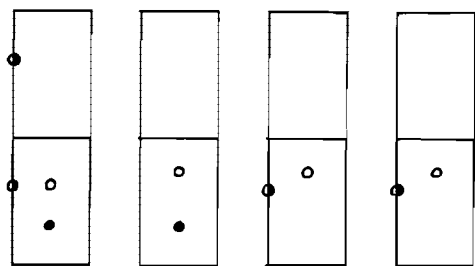
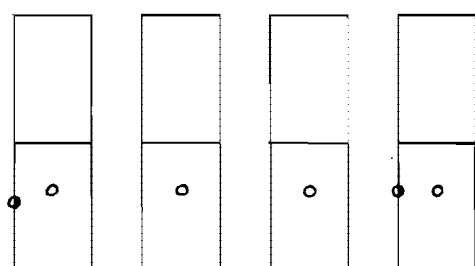
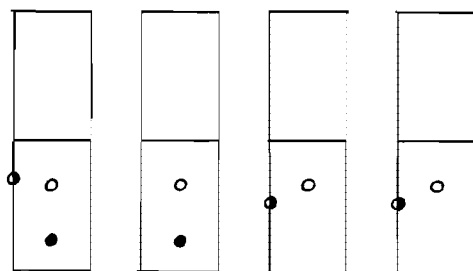
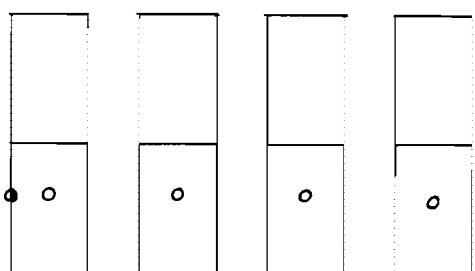
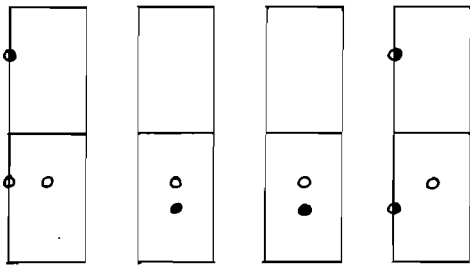
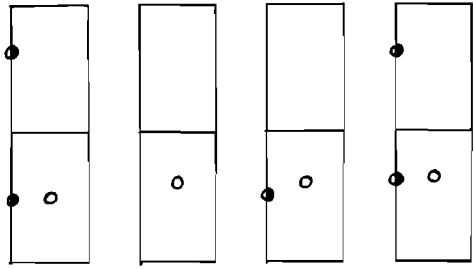
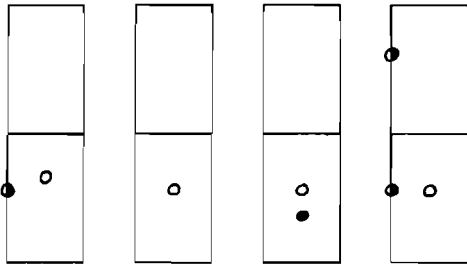
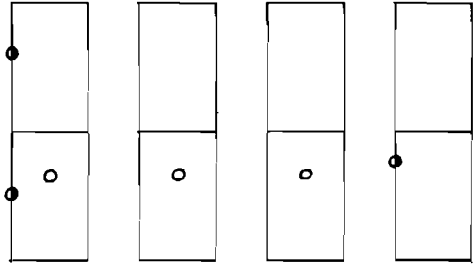
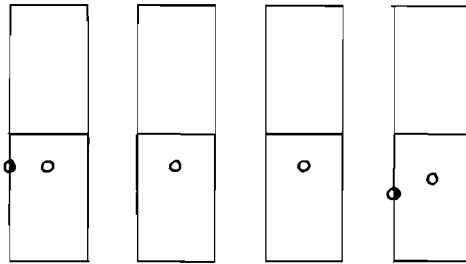
*G. group 1* (Table 1)*G. clelandi* Hirst, 1917*G. diversipilis* Hirst, 1926*G. gymnodactyli* Womersley, 1941*G. indica* Hirst, 1917*G. oedurae* Lawrence, 1936*G. gleadoviana* Hirst, 1926*G. keegani* Lawrence, 1953

Fig. 3.—For explanation see fig. 3 continued.

*G. simplex* Hirst, 1926*G. australis* Hirst, 1917*G. socotrensis* Hirst, 1917*G. group 2* (Table 1)*G. group 3* (Table 1)Fig. 3 continued.—Variation in chaetotaxy of the genu and femur in the genus *Geckobia* Megnin, 1878.

stout, long and spiculate. Presumably it is for this reason that the setal pattern differs from that found in the other species of the genus.

The same might be said of the tarsus which is also very long and tapered (fig. 5b). However, exactly the same setae, with one notable exception, are distinguishable as are found on the other genera. All other species of *Pterygosomidae* have a pair of dorsal terminal comb-like setae (*tdf*) at the apex of the tarsus. In *Hirstiella insignis*, however, this pair of setae is represented by a single flattened, fan-like, medio-dorsal seta (fig. 5b). The larva, nymph and adult female all show this character. The position and form of the seta strongly suggest, as implied above, that

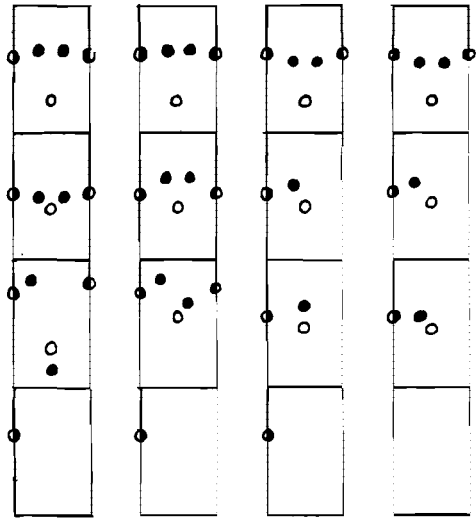
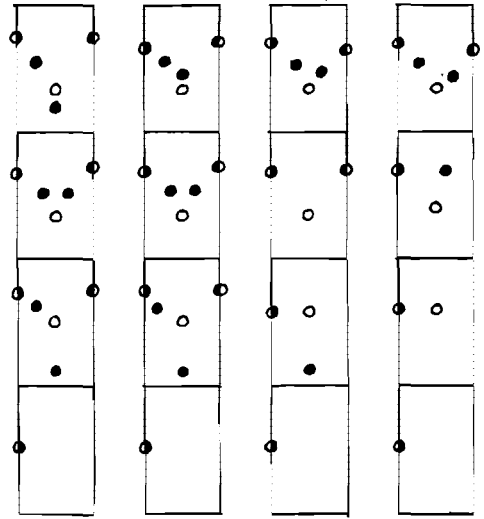
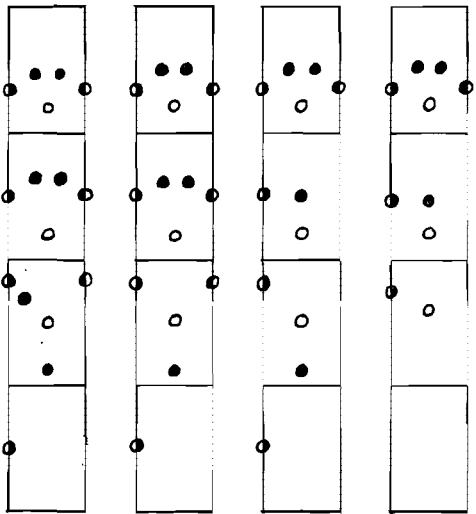
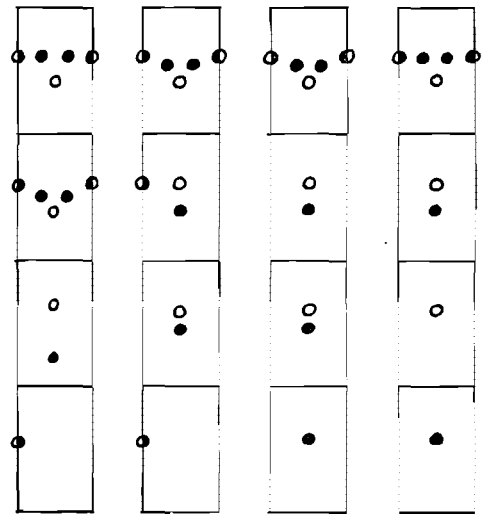
*H. trombidiformis* Berlese, 1920*H. insignis* (Berlese, 1892)*H. tenuipes* (Hirst, 1917)*H. stamii* Jack, 1961

Fig. 4.—Variation in chaetotaxy of the tibia, genu, femur and trochanter in the genus *Hirstiella* Berlese, 1920.

it is homologous to the comb-like setae of other species. Does it represent secondary fusion of a primitive pair of setae? This seems most unlikely by virtue of the manner in which setae are formed. Has one member of the pair been lost, the remaining seta assuming a median position afterwards? This seems more likely and may be correlated with space-shortage as mentioned above. However, its presence

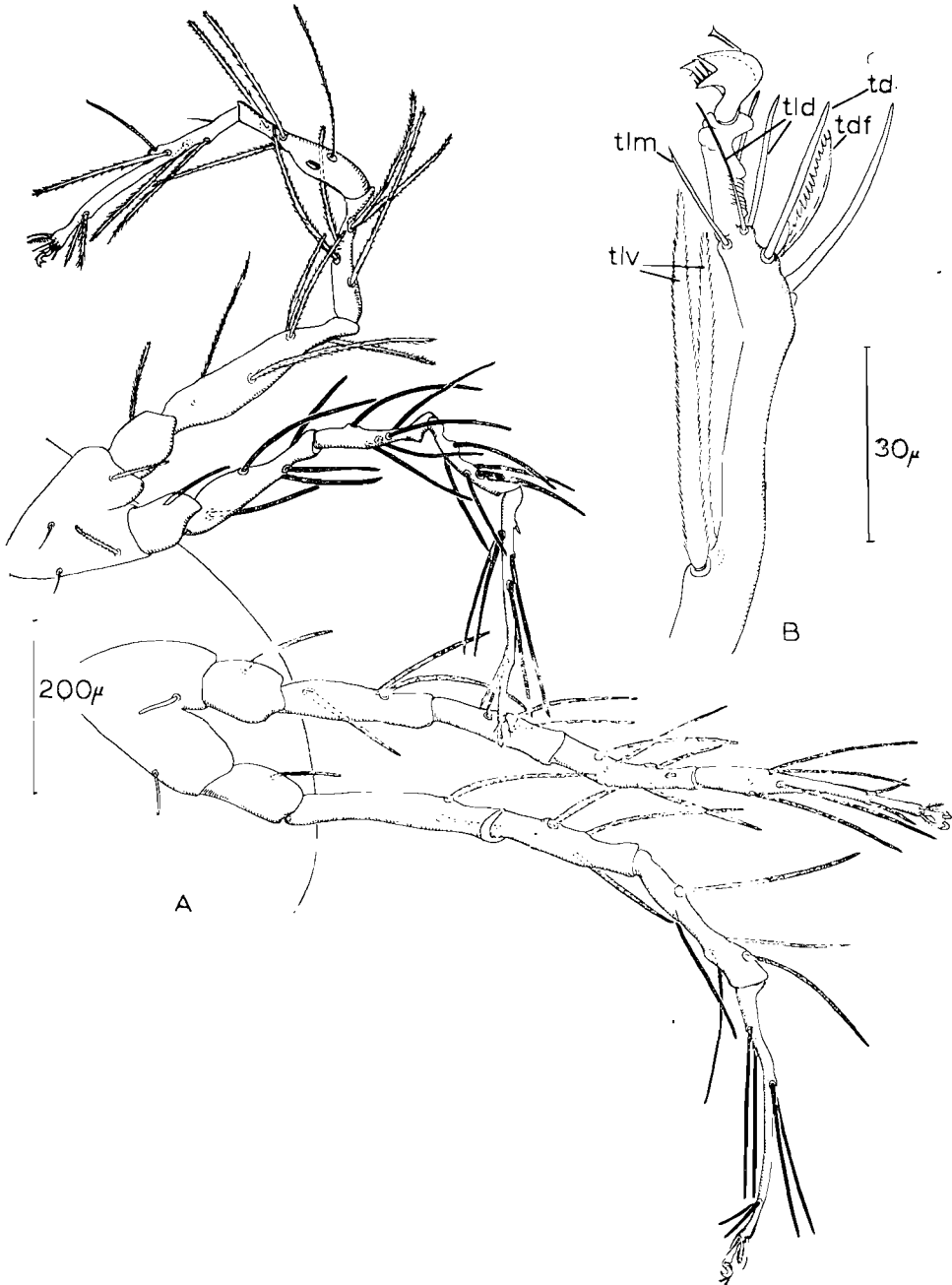


Fig. 5.—*Hirstiella insignis* (Berlese, 1892) Female. (a) Legs of the left side, ventral view; (b) Enlarged lateral view of the apex of tarsus I.

in all stages, especially the larva, might suggest a third possibility, namely that the single seta may be the primitive condition, the paired setae of other species being a secondary derivation. Some support for this hypothesis is gained from *Pimelia-philus cunliffei* Jack (1961) which lacks comb-like and fan-like setae, but which has a simple median dorsal seta immediately behind the pretarsus, in a corresponding position to that occupied by the fan-like seta of *H.insignis*.

At this point it is fitting to consider a viable female specimen of *Geckobiella texana* from Mexico, kindly supplied by Dr C. Yunker. This female was normal in all respects except that tibia III and tarsus II on one side of the body had developed abnormally. The tarsus especially is of interest in that it completely lacked the ambulacrum (fig. 6) and comb-like setae, having instead a stout conical spur. It was completely normal in respect of the remaining setae. Obviously such a teratological specimen must be interpreted with reservation, however, it does provide an interesting speculation. Could it be that interference with the process of normal ambulacrum formation also inhibits the formation of the comb-like setae? This would imply that the comb-like setae are not products of the tarsus but of the pretarsus or ambulacrum. All of the *Pterygosomidae* are bidactyl and lack all trace of the median claw, pulvillus or empodium. The two claws remaining are true lateral claws, clearly articulating with a basilar piece placed distally on the pretarsus and activated by tendons exactly as described by Grandjean (1939, 1941, 1943). This abnormal tarsus suggests the remote possibility that the fan-like seta of *Hirstiella insignis* is a migrated empodium. However, on this view two difficulties immediately arise. First the fan-like seta appears to be inserted on the tarsus and not the pretarsus; certainly not at all near the true claws. One might conceive this condition arising if the articulation of the pretarsus on the tarsus was very large, while the pretarsus itself was short. Such a concept however, leads directly to the second

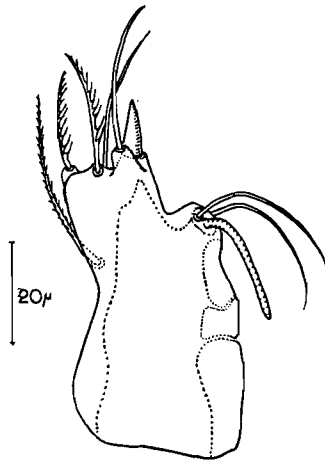


Fig. 6.—*Geckobiella texana* (Banks, 1904) Female. Teratological tarsus II, lateral view.

difficulty, namely that the region here termed the pretarsus could not in fact be homologous to the pretarsus of other mites. One must then suppose that the 'pseudo-pretarsus' of *Pterygosomidae* is a later expansion of the short primitive pretarsus. Such an interpretation appears clumsy in the extreme and unnecessarily difficult.

The specimen is of interest in other ways. Thus it seems possible, even likely in view of Dr Hughes' record of heteromorphic acarid males (1948, figs. 36, 47), that this condition is the result of a mutation. In which case two significant points follow. First that the effect of this mutation is asymmetrical, somewhat reminiscent of the condition in *Michaelichus* (*Analgosoidea*) where heteromorphic asymmetrical forms occur. Secondly it shows an extensive and sudden change of form and setal pattern in an individual which yet remained viable. This underlines the need for more studies on chaetotaxy and especially of infra-specific variation to assess the significance and reliability of these characters.

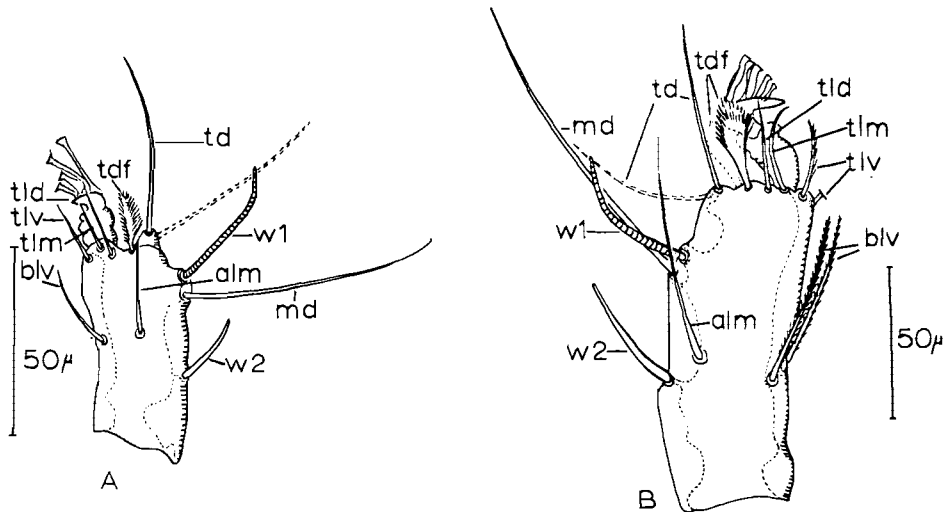


Fig. 7.—Tarsal setation in the Pterygosomidae. Tarsus I, Lateral views of (a) *Hirstiella stamii* Jack, 1961 and (b) *Geckobiella texana* (Banks, 1904).

The tarsal setae of other species and genera follow a quite definite pattern which is shown fully by tarsus I of *Hirstiella stamii* and *Geckobiella texana* (fig. 7). Reduction in the number of tarsal setae occurs from genus to genus, from species to species within a genus, and indeed from leg I to leg IV on any particular species. Birefringent 'poils ordinaires' of Grandjean or 'scobalae' of Southcott are found together with the isotropic solenidia. The occurrence of these setae is shown in table 2.

Reference to fig. 7 will show the setae designated by the symbols used in table 2. Paired setae are enclosed in brackets. Where one of the pair is missing then the brackets are simply omitted. In these circumstances the remaining seta usually

occupies a median position. The following symbols are used in designating the tarsal setae.

- (*td*) terminal dorsal simple setae (always paired).
- (*tdf*) terminal dorsal fan-like setae (paired except in *H. insignis*).
- (*tl**d*) terminal latero-dorsal setae (paired and smooth or spiculate).
- (*tl**m*) terminal mid-lateral setae (usually paired, smooth or spiculate, on tarsus I only).
- (*tl**v*) terminal latero-ventral setae (paired and smooth or spiculate).
- (*bl**v*) basal latero-ventral setae (paired or single, smooth or spiculate).
- alm* mid antero-lateral unpaired seta (smooth or spiculate, on tarsus I only, commonly missing entirely).
- md* Unpaired median dorsal seta (associated with the sensory clavate solenidion of tarsus I).
- w*¹ The baculiform solenidion on tarsi I-III.
- w*² The basal solenidion of tarsus I in certain genera.
- w**r* The reduced or small striated solenidion on tarsus III of certain genera, often claviform.

At present I am not certain how far the homologies of various setal types and patterns can be traced between the *Pterygosomidae* and the varied genera studied by Professor Grandjean. For this reason an arbitrary system of designation is used which is not intended to imply homology in any way with Grandjean's setae. Later when more investigations are completed I hope to translate them into terms of Grandjean's and Southcott's systems.

Of major importance in Grandjean's system is the recognition of true hairs, poils ordinaires etc. the scobalae of Southcott, from sense organs, some of which may be hair-like. All of these sense organs, with the exception of the solenidia, are birefringent and all contain a protoplasmic core which pierces the base of the organ.

The system of notation used here does not distinguish between scobalae and sense organs except for the baculiform solenidia of tarsi I and II and the claviform solenidion of tarsus III of *Hirstiella tenuipes*, *H. stamii* and the genus *Geckobiella*. These solenidia are transversely striated and quite unmistakable. From examination of the very few larvae and deutonymphae known in this family, it seems likely that this solenidion is represented in all of these developmental stages and thus corresponds to omega 1 (ω^1) of Grandjean (1935) in the oribatids. However, it also seems likely that other unstriated solenidia are present which appear more hair-like. Preliminary examination with polarized light shows that the dorsal tibial seta is isotropic, together with a number of tarsal setae. In one case at least, one spiculated seta (*td*) of the pair on tarsi I and IV appeared isotropic. Whether this represents a new kind of solenidion or an excessive demand on the simple polarizing equipment available, I am at a loss to say. Unfortunately space considerations prohibit the detailed treatment which the tarsi well merit. Nevertheless one cannot but be impressed by the relatively simple setal pattern which holds throughout the

TABLE 2.—TARSAL CHAETOTAXY IN THE PTERYGOSOMIDAE

Generalized formula:	TARSUS I										TARSUS II						TARSUS III			
	(td)	(tdf)	(tld)	(tlm)	(tlv)	(blv)	alm	md	w ¹	w ²	(td)	(tdf)	(tld)	(tlv)	(blv)	w	(td)	(tdf)	(tld)	(tlv)
<i>Hirstiella</i>	*	*	*	*	*	*	0	*	*	*	*	*	*	*	mv	*	*	*	*	*
<i>H. trombidiformes</i>	*	tdf	*	*	*	*	0	*	*	*	*	tdf	*	*	*	*	*	tdf	*	*
<i>H. insignis</i>	*	*	*	*	*	*	*	*	*	0	*	*	*	*	*	*	*	*	*	*
<i>H. tenuipes</i>	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
<i>H. stamii</i>	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
<i>Geckobiella</i>	*	*	*	*	*	*	*	*	*	*	*	*	*	*	mv	*	*	*	*	*
<i>G. texana</i>	*	*	*	*	*	*	*	*	*	0	*	*	*	*	mv	*	*	*	*	*
<i>G. harrisi</i>	*	*	*	*	*	*	*	*	*	0	*	*	*	*	mv	*	*	*	*	*
<i>Ixoderma</i>																				
<i>I. inverta</i>	td	*	*	*	*	mv	*	*	*	0	td	*	*	*	mv	*	td	*	*	*
<i>Scaphothrix</i>																				
<i>S. convexa</i>	*	*	*	*	*	*	*	*	*	0	*	?	*	*	*	?	*	*	*	*
<i>Zonurobia</i>																				
<i>Z. polyzonensis</i> ..	*	*	*	*	*	*	*	*	*	0	*	*	*	*	mv	*	*	*	*	*
<i>Z. group A</i>	*	*	*	*	*	*	0	*	*	0	td	*	*	*	mv	*	td	*	*	*
<i>Z. group B</i>	td	*	*	*	*	*	0	*	*	0	td	*	*	*	mv	*	td	*	*	*
<i>Gerrhosauroidia</i>																				
<i>P. (G.) bicolor</i> }	*	*	*	*	*	*	0	*	*	0	td	*	*	*	mv	*	td	*	*	*
<i>P. (G.) hystrix</i> }	*	*	*	*	*	*	0	*	*	0	td	*	*	*	mv	*	td	*	*	*
<i>Pterygosoma</i>																				
<i>P. group A</i>	*	*	*	*	*	*	0	*	*	0	td	*	*	*	mv	*	td	*	*	*
<i>P. group B</i>	*	*	*	*	*	mv	0	*	*	0	td	*	*	*	mv	*	td	*	*	*
<i>Geckobia</i>																				
<i>G. group A</i>	*	*	*	*	*	*	*	*	*	0	*	*	*	*	*	*	*	*	*	*
<i>G. group B</i>	*	*	*	0	*	*	*	*	*	0	*	*	*	*	*	*	*	*	*	*

Key: * indicates setae present as in generalized formula. 0=absent. ?=doubtful. If brackets omitted and seta indicated (e.g. td) then only one of the pair of setae

Zonurobia group A: *Z. debilipes*, *Z. cordylensis*, *Z. montana*, *Z. transvaalensis*, *Z. sanguinolenta*, *Z. semilunaris*, *Z. circularis spiniventer*.*Zonurobia group B:* *Z. subquadrata*, *Z. circularis circularis*, *Z. circularis latior*, *Z. circularis capensis*, *Z. circularis longipilis*.*Pterygosoma group A:* *P. persicum*, *P. mutabilis*, *P. caucasica*, *P. annectans*, *P. tenuisetis*, *P. spinosa*, *P. serrata*, *P. agamae*.*Pterygosoma group B:* *P. transvaalense*, *P. riangulare*, *P. hirsti hirsti*, *P. hirsti bedfordi*, *P. fimbriata problematica*, *P. benguellae*, *P. melanum melanum*, *P. melanum capensis*, *P. melanum angolae*, *P. bibronii bibronii*, *P. bibronii pseudorbicularis*, *P. inermis inermis*, *P. adramitana*, *P. tuberculata*, *P. dioura*, *P. agamae aculeatum*, *P. dracoensis*.*Geckobia group A:* *G. clelandi*, *G. fitzsimonsi*, *G. gehyrai*, *G. hemidactyli*, *G. hewitti*, *G. hindustanica*, *G. karrooica karrooica*, *G. loricata*, *G. latasti*, *G. philippinensis*, *G. phyl**G. tarentulae*, *G. indica*, *G. diversipilis*, *G. gleadowiana*, *G. papuana*, *G. socotrensis*, *G. capensis capensis*, *G. oedurae*, *G. naultina*, *G. keegani*, *G. gymnodacty**Geckobia group B:* *G. homopholis*, *G. turkestanica*, *G. malayana*, *G. simplex*, *G. haplodactyli*, *G. australis*, *G. pachydactyli*, *G. namaquensis*, *G. transvaalensis*, *G. rhoptropi*.

family, its constancy through widely differing genera drawn from a large variety of hosts and from an immense geographical area. The conclusion, that this family is of monophyletic origin seems inescapable and supports evidence of other characters such as the form of the mouthparts and the similarity of larval forms.

PRÉCIS OF TENTATIVE FINDINGS

(1) In terms of leg chaetotaxy, the genus *Hirstiella* shows considerable variation. This is supported by consideration of the form of the chelicerae pedipalps, the claws, the form and size of the dorsal idiosomal setae and the form of the legs. The genus appears to show progressive adaptation to life beneath the scales of the host.

(2) The remaining genera are adapted to lizard parasitization in three main ways:

- (a) In *Geckobiella* by attaching beneath two adjacent scales while yet retaining an elongate body and few idiosomal setae.
- (b) In *Pterygosoma*, *Gerrhosauroidia*, *Zonurobia*, *Scaphothrix* and *Geckobia* by attaching beneath a single scale, the body showing more or less marked allocotogenesis and, except for *Scaphothrix*, idiosomal hypertrichy.
- (c) In *Ixodiderma* and certain species of *Pterygosoma* and *Zonurobia*, by attaching between scales or in scale-less regions, leaving the body more or less completely exposed. Such forms are usually circular and flattened, or spherical in shape and have a thicker cuticle and reduced hypertrichy. The same habit is found in many species of *Geckobia*, which may or may not show allocotogenesis and which all show idiosomal hypertrichy and a thin cuticle. In this case the small body size appears to be of adaptive significance.

(3) It seems possible that there is a correlation between size, thickness of cuticle and number of body setae in the specialized genera, though not in *Hirstiella*. Thus *Geckobiella* is relatively large, has few idiosomal setae and thin cuticle. *Ixodiderma*, *Pterygosoma caucasica* and *P. gracilipalpis* have a thick cuticle and relatively few short idiosomal setae. Most of the other species of *Pterygosoma*, *Geckobia* and *Zonurobia* show a thin cuticle, large numbers of idiosomal setae which are often elongated or broadly expanded. This does not hold for *Scaphothrix* which has few setae and only a moderately stout cuticle.

(4) There also seems to be a correlation between reduction in numbers of leg setae and idiosomal hypertrichy.

(5) The reduction of leg setae from genus to genus within the family appears to be correlated with a more specialized habit as a scale-mite. The significance of the similar reduction in numbers of leg setae found between different species in the same genus is not known. Finally there is a reduction in numbers of leg setae from leg I to leg IV of any particular species which is also ambiguous. In the highly specialized genera such as *Geckobia*, *Pterygosoma* and *Zonurobia* we might expect a concentration of sensory setae on tarsus I for location of the attachment area

or of a mate in the case of the male. Such an adaptation for the anterior end of the body in bilaterally symmetrical animals is very common. However, once attached, the most likely source of new stimuli, in the case of the female at least, is from predators and mates and from the rear. We might therefore expect to find some retention or secondary development of sensory hairs on leg IV of these more specialized genera. This is not found. Progressive reduction of setae occurs from leg I to leg IV in this group as in those studied by Grandjean and others. Could this be the expression of an orthogenetic trend in the Acari? It is difficult to envisage in what circumstances it could be positively selected for in such widely divergent groups of such equally widely divergent habits.

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SUMMARY

The family *Pterygosomidae* is briefly reviewed, together with the habits evolved in the different genera. The chaetotaxy of the tibia, genu, femur and trochanter is compared in the different genera and the major variations in each genus are described. Progressive reduction in numbers of setae is found from leg I to leg IV in each species, from species to species in each genus and from genus to genus within the family. Especial mention is made of *Hirstiella insignis* Berlese (1892) which shows many atypical features. A teratological tarsus II of *Geckobiella texana* Banks (1904) is described which shows some similarity to that recorded for certain heteromorphic acarid males. Some preliminary observations on the tarsal setation are summarized in tabular form. Finally a discussion and a précis of tentative findings are presented.

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